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Interspecific variation in *Apodemus* from the northern Adriatic islands of Yugoslavia

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Abstract

Reevaluated the systematic position of the endemic species *Apodemus krkensis* from the island Krk in Croatia, Yugoslavia.

Three hundred and thirty-two museum specimens of *Apodemus sylvaticus* (wood mouse) and *A. flavicollis* (yellow-necked mouse) from 10 insular, coastal, and inland localities in northwestern Yugoslavia were compared to seven specimens of the nominal species *A. krkensis* collected in 1975 near the type locality of Baška on the island of Krk. Results of a multivariate analysis of variance using 11 cranial characters showed *A. sylvaticus* could be distinguished with ease from *A. flavicollis* but that it was inseparable morphologically from *A. krkensis*. The only demonstrable difference between *A. sylvaticus* and *A. krkensis* was the gray pelage possessed by the latter. Microscopic examination of hairs from the dorsal pelage suggested that this variation in color centers around a reduction in pigment deposition and the number of melanosomes (pigment granules) synthesized by hairs of the underfur in *krkensis*. The paling effect is attributed to introduction of a mutant allele at the C (albino) locus. Inasmuch as additional collecting on northern Adriatic islands and the adjacent mainland has shown the gray form to be more widespread than previously thought, and because it occurs

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sympatrically with normally colored *sylvaticus* and there is no evidence that the two are reproductively isolated, *A. krkensis* is considered to be a color morph of, and conspecific with, the wood mouse *A. sylvaticus*.

Introduction

Field mice of the genus *Apodemus* are a distinctive group of murid rodents ranging throughout the Palearctic and Oriental regions. Of the 12 species currently recognized by Corbet (1978), *A. krkensis* is the least well known. It has been recorded only from the type locality of Baška on the island of Krk, and until this study was represented by only the three specimens of the type series (Mirić 1968). During the summer of 1975, a joint Yugoslav-American field team working on the island of Krk in the northern Adriatic collected seven animals that, based on the gray coloration of the pelage and a series of cranial characters presented in the original description, appeared assignable to this nominal species. A striking similarity between these specimens and those of *A. sylvaticus*, with which it is sympatric, prompted us to review the taxonomic status of *A. krkensis*. In doing so we have used two similar species, *A. flavicollis* (yellow-necked mouse) and *A. sylvaticus* (wood mouse), for comparisons of morphology and pelage. Comparative samples were drawn from selected mainland localities as well as the islands of Krk and Rab in order to establish limits of geographic and populational variation.

It should be noted that the type series of *A. krkensis*, which is housed in Beograd, Yugoslavia, was unavailable to us for examination. As a consequence, conclusions reached herein must be regarded as tentative until such time as the holotype and paratypes can be studied. However, Mirić (1968) provided a very detailed diagnosis of the taxon and our specimens fit his description in every feature. There is little doubt that the mice collected in 1975 represent additional records of *A. krkensis*.

Material and methods

This study was based on the examination of 339 museum specimens from the Republic of Croatia, Yugoslavia; all specimens currently are housed in the mammal collection of The Museum, Texas Tech University, Lubbock, Texas. General collecting sites, the number of animals examined, and the locality number assigned to each sample for the analysis (see Fig. 1) are as follows: *A. flavicollis*, Lekenik (103), locality 1; Senj (9), locality 7; Rab (9), locality 8; Posedarje (2), locality 9. *A. sylvaticus*: Posedarje (41), locality 2; Krk (100), locality 3; Rab (34), locality 4; Labin (11), locality 5; Senj (22),

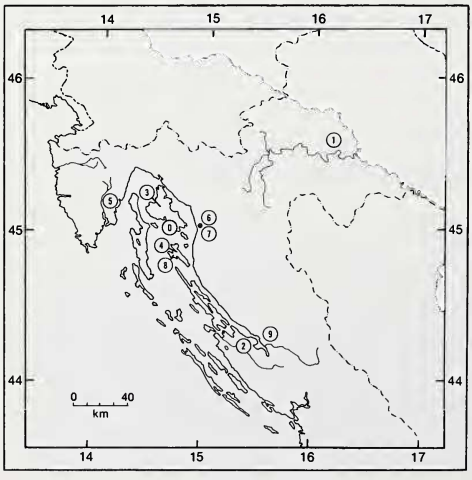

Fig. 1. Localities of *Apodemus* sampled in this study from the Republic of Croatia in Yugoslavia. See text for explanation of numerals

locality 6. *A. krkensis*: Krk (7), locality 0. A detailed listing of the precise collecting localities for all specimens is on file at The Museum, Texas Tech University, and is available to interested persons on request. However, because specimens of the nominal species *A. krkensis* are rare, the localities and numbers of individuals taken from each are given here (distances are recorded in kilometers, km., from the town of Krk, and elevations are noted in meters, m.): 2.2 km. N, 5.4 km. E Krk, 175 m., 1; 2.6 km. S, 9.8 km. E Krk, 150 m., 1; 3.6 km. S, 4.8 km. E Krk, 100 m., 3; 4.7 km. S, 5.4 km. E Krk, 150 m., 2. A total of 14 external and cranial measurements were recorded for each individual included in the analysis: total length, tail length, hind foot length, greatest length of skull, condylobasal length, cranial depth, zygomatic breadth, cranial breadth, interorbital breadth (least), nasal length, length of incisive foramine, length of molar toothrow, breadth across molars (greatest), length of nasofrontal. All cranial measurements were made to the nearest 0.1 millimeter with the aid of dial calipers. External dimensions were taken directly from museum specimen labels.

Specimens were assigned to one of five age categories based on wear on the molar teeth. Classes were defined as: Class 0: little tooth wear evident, dentine not exposed, M3 with cusps distinct; Class 1: dentine exposed on most cusps, especially on M3, little wear on M2, no wear apparent on M1; Class 2: cusps on M3 forming serpentine enamel lophs, wear evident on M2 but not particularly noticeable on M1; Class 3: dentine on M2 making a continuous unbroken loop, cusps and enamel lophs still visible on M1; Class 4: central lophs entirely worn away on M3, M2, and M1.

Individual, age, and secondary sexual variation were analysed with the statistical analysis system (SAS) designed and implemented by Barr et al. (1976). Means were calculated for each character noted above and a one-way analysis of variance was used to test for differences among age classes and between sexes for each locality. If means were found to be significantly different, Duncan's multiple range test was applied to identify maximally nonsignificant subsets. Coefficients of variation (CV) were calculated to determine the extent of character variability.

Geographic variation was analyzed by means of univariate (mean, standard deviation, standard error) and multivariate statistics. To assess the degree of divergence among localities with all characters considered simultaneously, a multivariate analysis of variance (Manova) in SAS was used. This program provided weighted combinations of the measurements, which maximized the distinction between groups. Significant differences between groups were not assumed a priori, however. Four criteria (Hotelling-Lawley's Trace, Pilla's Trace, Wilke's Criterion, and Roy's Maximum Root Criterion) were used to test the hypothesis of no overall locality effect, that is, no significant morphological differences between or among samples. Characteristic roots and vectors were then extracted and mean canonical variates computed for each locality. New orthogonal axes, termed canonical variates, were constructed to extract the next best combination of characters to discriminate among samples. Characters with the least within-sample and greatest between-sample variation were emphasized. Each eigenvalue and its corresponding canonical variate (characteristic root) represent an identifiable fraction of the total variation. Sample means and individuals were plotted on those canonical variates that accounted for the greater fractions of total variation. The relative importance of each original variable to a particular canonical variate was computed by multiplying the vector variable coefficient (eigenvalue) by the mean value of the dependent variable, summing all variable values for a particular vector, and then calculating the per cent relative influence (per cent loading) of each variable per vector. Variation in the coloration of the middorsal pelage was examined with a Bausch and Lomb Spectronic 505 recording spectrophotometer equipped with a visible reflectance attachment. Trichromatic coefficients (X, Y, Z) were derived by the 10 selected ordinate method from curves of percentage reflectance in the range of wavelengths from 400 to 700 nanometers. This was done using the trichromatic coefficient computing chart for illuminant C produced by Bausch and Lomb. Specimens used in the color determination were selected to represent the entire range of variation interspecifically and geographically. Comparisons also were made, using a Nikon compound microscope without a filter attachment, of individual dorsal hairs in order to determine if differences in morphology or pigment distribution existed.

Results

Of the three forms of nongeographic variation (age, secondary sexual, individual) examined, analysis of variance revealed significant differences due to sex and age in all species at all localities. To minimize these influences, sexes were treated separately and only tooth wear classes 3 and 4 included in the subsequent analysis of geographic variation.

Individual variability was not pronounced in any character examined. Coefficients of variation for all characters ranged from 2.1-8.9 and were well within the limits of those reported for other small rodents (Long 1968). Cranial measurements, however, were

consistently less variable; for this reason, interpopulational and specific comparisons were restricted to the use of cranial characters.

Table 1

Mean followed by range, in parentheses, sample size, and standard error of the mean of selected cranial and external characters for adults of three nominal species of *Apodemus* from the Republic of Croatia, Yugoslavia

Localities from which samples were taken are: *A. flavicollis*, Lekenik; *A. sylvaticus*, Island Krk; *A. krkensis*, Island Krk. Measurements in italics are for a juvenile

			A. krkensis	
Character	*A. flavicollis*	*A. sylvaticus*	Topotypes	Types
Greatest length of skull				
Males	28.2 (26.8–29.4) n = 19, 0.20	26.9 (25.3–28.0) n = 37, 0.11	26.4 (25.0–27.7) n = 2, 0.14	27.2., *24.6*
Females	27.2 (25.7–28.5) n = 11, 0.28	26.2 (24.3–27.2) n = 22, 0.15	25.5 (24.4–26.2) n = 3, 0.06	27.3
Condylobasal length				
Males	25.6 (24.2–26.8) n = 19, 0.19	24.0 (22.9–24.9) n = 36, 0.09	23.7 (22.5–24.8) n = 2, 0.12	25.0, *22.4*
Females	24.7 (23.3–26.1) n = 11, 0.30	23.4 (21.5–24.7) n = 22, 0.15	22.7 (21.9–23.2) n = 3, 0.04	24.9
Zygomatic breadth				
Males	14.2 (13.1–15.0) n = 19, 0.12	13.3 (12.4–13.9) n = 36, 0.06	13.1 (12.9–13.2) n = 2, 0.02	13.5, *12.7*
Females	13.8 (12.9–14.3) n = 12, 0.14	13.1 (12.4–13.8) n = 20, 0.09	12.5 (12.1–12.8) n = 3, 0.02	13.7
Cranial breadth				
Males	12.1 (11.6–12.7) n = 19, 0.06	12.0 (11.3–12.5) n = 37, 0.05	11.8 (11.7–11.9) n = 2, 0.01	12.1, *12.0*
Females	11.9 (11.3–12.6) n = 12, 0.11	11.9 (11.0–12.4) n = 22, 0.07	11.7 (11.6–11.8) n = 3, 0.01	12.4
Interorbital breadth				
Males	4.3 (4.1–4.8) n = 19, 0.04	4.3 (4.0–4.6) n = 37, 0.02	4.3 (4.2–4.3) n = 2, 0.01	4.3, *4.2*
Females	4.2 (3.9–4.6) n = 12, 0.07	4.2 (3.8–4.8) n = 23, 0.04	4.0 (3.9–4.2) n = 3, 0.01	4.3
Total length				
Males	215.9 (202–236) n = 16, 2.53	199.0 (180–227) n = 36, 1.74	193.5 (190–197) n = 2, 0.35	*176*
Females	211.3 (192–238) n = 11, 4.23	191.1 (165–205) n = 21, 2.14	183.0 (174–192) n = 2, 0.90	
Tail length				
Males	107.7 (98–122) n = 16, 1.55	99.4 (94–111) n = 36, 1.06	94.5 (88–101) n = 2, 0.05	*83*
Females	106.6 (92–122) n = 11, 2.88	95.2 (89–102) n = 21, 0.79	90.5 (83–98) n = 2, 0.75	
Hind foot length				
Males	24.1 (23–25) n = 19, 0.14	22.7 (19–24) n = 37, 0.13	22.5 (22–23) n = 2, 0.50	24.1, *22.5*
Females	23.3 (21.5–25) n = 12, 0.36	22.7 (19–24) n = 23, 0.13	22.5 (22–23) n = 3, 0.50	22.4

Morphology

Specimens examined in the geographic portion of the analysis were pooled into the grouped geographic localities shown in Fig. 1. To reiterate, *A. flavicollis* was represented by localities 1, 7, 8, and 9, *A. sylvaticus* by localities 2, 3, 4, 5, and 6, and *A. krkensis* by locality 0. Standard statistics (mean, range, standard deviation, and standard error) were calculated by species for all external and cranial measurements. Data for selected measurements from representative samples of adults are presented in Table 1.

In general, specimens of *A. flavicollis* averaged larger in all measurements, but no significant morphological differences were detectable between *A. sylvaticus* and *A. krkensis* for any character examined. Little intraspecific variation among populations was noted. All external and cranial characters were highly homogeneous within species and differences between mainland and insular populations were not evident.

To determine the amount of variation among samples and species considering all cranial characters simulataneously, a multivariate analysis of variance (MANOVA) was used and four criteria (Hotelling-Lawley's Trace, Pilla's Trace, Wilke's Criterion, and Roy's Maximum Root Criterion) were applied to test the hypothesis of no overall locality effect. All four criteria produced F-values that were highly significant at $p \leq 0.0001$. Thus, significant morphological differences among samples were assumed to be due to the effect of locality or species.

To identify the source and nature of this variation, 11 canonical variates were extracted. The first canonical variate expressed 63.66 per cent of the phenetic variation in males, 53.97 per cent in females; the second, 14.67 for males and 20.15 for females. Thus, more than 74 per cent of the total phenetic variation for males and more than 84 per cent of the variation for females was accounted for by the first two eigenvectors among the 10 samples of *Apodemus* studied. A two dimensional plot of vectors I and II (including the mean and one standard deviation on either side of the mean for each sample) is presented in Fig. 2. Only males are figured because almost identical results were obtained for females; localities 8 and 9 were not included because insufficient adult mice were available. Examination of Fig. 2 reveals two major groupings within the character space, labeled A and B. Group A consists of samples of *Apodemus sylvaticus* from the islands of Krk and Rab and the Yugoslavian mainland (localities 2–6) and the single sample of *A. krkensis* (locality 0) from the southeastern end of the island of Krk. Group B contains samples of *A. flavicollis* from the island of Rab and the mainland (localities 7 and 1). No overlap occurs between samples of these two clusters. This is especially interesting in light of the position of *A. krkensis* in this

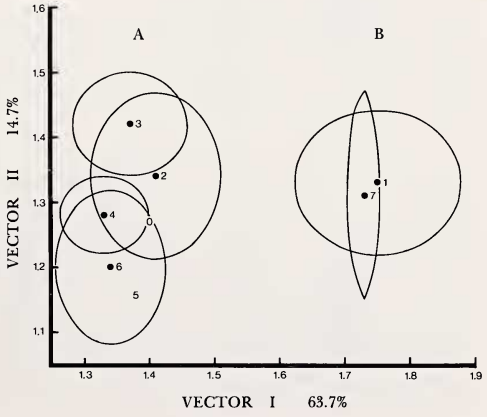

Fig. 2. A two dimensional plot of the first two canonical variates derived from a multivariate analysis of variance of 11 cranial characters in males of three nominal species of *Apodemus*. Means and one standard deviation about the mean are shown; numerals refer to localities sampled. Numbers without ellipses represent samples of only one individual

figure. The tight association of this species with samples of *A. sylvaticus* in group A indicates that these two taxa cannot be separated consistently on the basis of morphology even when all characters are compared simultaneously.

The relative contributions of each character to the first two canonical variates are given in Table 2. Vector I primarily separates groups A and B. Vector II tends to distinguish samples within the two groupings from each other, although no distinct subclusters are evident.

Condylobasal length, greatest length of skull, zygomatic breath, and interorbital breadth load heaviest on vector I; thus samples in group A have shorter and narrower skulls than those in group B. Cranial breadth, breadth across the molars, length of the nasofrontal bones, and condylobasal length exert the heaviest influence on vector II.

Table 2

Eigenvalues of canonical variates I and II showing the percentage influence of each cranial character in males of three nominal species of *Apodemus*

Eigenvalues shown represent the normalized vector coefficient of each character. The median is a value in millimeters that reflects an approximate midpoint between the largest and smallest actual measurement of each character

		Vector I		Vector II	
Character	Median	Eigen-value	Percent Influence	Eigen-value	Percent Influence
Greatest length of skull	27.1	−0.0833	15.66	0.0478	8.00
Condylobasal length	24.3	0.1403	23.73	−0.1013	15.26
Cranial depth	9.9	0.1026	7.10	−0.0317	1.98
Zygomatic breadth	13.4	0.1316	12.25	−0.0384	3.16
Cranial breadth	11.9	−0.0855	7.13	0.2122	15.70
Interorbital breadth	4.3	−0.4136	12.32	0.0209	0.57
Nasal length	10.2	0.0284	2.02	0.2249	14.27
Length of incisive foramine	5.5	−0.2573	9.88	−0.2217	7.60
Length of molar toothrow	3.9	0.3076	8.42	−0.0986	2.40
Breadth across molars	5.5	−0.0177	0.67	0.4602	15.62
Length of nasofrontal	19.4	0.0061	0.82	−0.1286	15.44

Pelage

Visual assessment of adult coat color suggested that populations of *A. flavicollis* were strikingly homogeneous. Differences among localities or between sexes were not found, and animals were consistently rusty brown dorsally and white ventrally with a marked transition between dorsum and venter. An orange throat patch was found in 97 per cent of the mice examined.

A. sylvaticus differed from *A. flavicollis* in having less red in the fur, a dingy white to grayish belly, and a poorly defined dividing line between the dorsal and ventral pelage. Although *A. sylvaticus* failed to show sexual dimorphism in coloration it did exhibit variation in color between localities. Proceeding from north to south among the mainland localities examined in this study, there was a slight shift from a reddish to orangish wash on the fur, which gave the overall illusion of a paling of the coat. On the island of Rab, mice resembling mainland populations in their darker coloration were found intermingled with pale gray animals. On the neighboring isle of Krk, these gray mice heretofore have been referred to the species of *A. krkensis.*

In the spectrophotometric analysis of the middorsal pelage, sample size was small (*A.*

krkensis, Krk, 2; *A. sylvaticus*, Rab, 3; *A. sylvaticus*, Krk, 2) because only the extremes – that is, the darkest and palest individual – were selected from each locality. This was done in order to bracket completely the range of variation shown within a population. Fig. 3 presents the results of this analysis. At low wavelengths (400–500 nanometers), *A. krkensis* produced the highest reflectance values, indicating that of the three samples tested it was the palest. It is noteworthy that *A. sylvaticus* examined from Rab fall in an intermediate position on Fig. 3 between *A. sylvaticus* on Krk and *A. krkensis*. A measure of the red component in the fur is given by the change in slope between the lower and higher wavelengths. *A. krkensis* shows almost a linear relationship between per cent reflectance and wavelength over the entire range scanned, pointing to the fact that *krkensis* is primarily gray and lacks any reddish pigment in its hairs. *A. sylvaticus* from Krk, on the other hand, exhibits a rapid increase in reflectance at wavelengths above 500. Mice from Rab also produce a change in reflectance readings over 500, which again indicates the presence of some red in the pelage. The higher reflectance values of *A. sylvaticus* on Rab relative to *A. sylvaticus* on Krk at wavelengths between 400 and 500, however, suggests that there are some very pale colored mice on Rab and that even though some animals have red in the fur it is not as rich as that found in conspecifics on Krk.

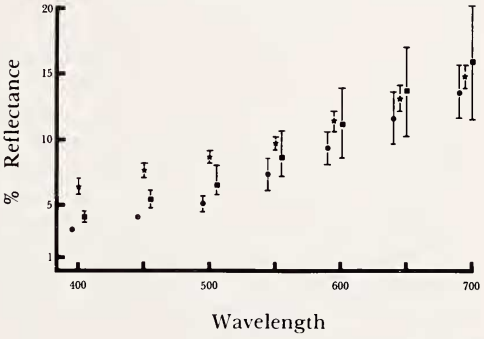

Fig. 3. Spectrophotometric analysis of the middorsal pelage in two species of *Apodemus* (wavelength in nanometers). Stars = *A. krkensis* from the island Krk; squares = *A. sylvaticus* from the island Rab; circles = *A. sylvaticus* from the island Krk. Plotted are the extremes (vertical bars) and means in color variation noted among the mice from each locality

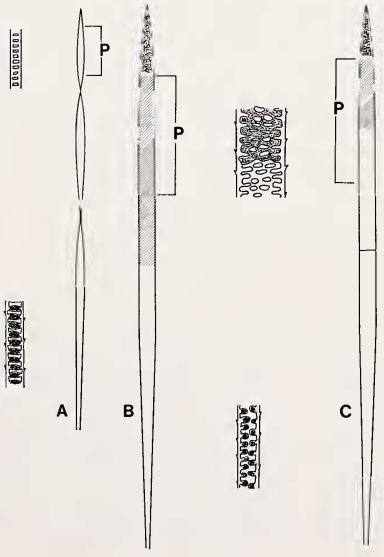

Fig. 4. Schematic diagram of the underfur (A) in *Apodemus sylvaticus* and *A. krkensis*, and the guard hairs in *A. sylvaticus* (B) and *A. krkensis* (C). P, refers to the distribution of phaeomelanin in medullary cells. Insets show the position of air spaces in the medulla and the localization of pigment granules in the base of the hair shafts. The upper right inset illustrates the appearance of dark (above) and clear (below) reticulated patterns formed by keratin in the guard hairs

A microscopic examination of the hairs of *A. sylvaticus* reveals there are two distinct types (Fig. 4). Hairs of the underfur (A) outnumber guard hairs (B, C) approximately 10 to one; are long and narrow, seemingly cylindrical in shape, and tricolored; and bear two conspicuous constrictions that subdivide the shaft into three segments. Insets show the position and shape of intramedullary air spaces and the localization of pigment granules (lower inset). Both eumelanic (brown) and phaeomelanic (yellow) pigment granules are present and are distributed as follows: the distal tip contains eumelanin in the cortex and medulla; a narrow band of yellow pigment, confined to the medulla, begins just above the distal-most constriction but terminates at the dark distal tip; the remainder of the shaft is eumelanic with pigment granules densely packed and occurring primarily in the medulla. The general appearance of the underfur, proceeding from the base upward, is a slate gray shaft, yellow to orangish distal band, and a dark tip. Where the terminal phaeomelanic band and eumelanic tip merge, the hair takes on a reddish hue. Underfur from *A. krkensis* is indistinguishable morphologically from that described for *sylvaticus* above. However, the pigment appears neither as dark nor the granules as numerous as in *sylvaticus*. Consequently, all the bands described are considerably paler in *krkensis*.

Guard hairs also are tricolored (in terms of patterns of pigment distribution) and are almost of the same length as hairs of the underfur but are appoximately three times wider, anteroposteriorly flattened, and without constrictions. Eumelanin is found in the medulla of the proximal half of the shaft and in the medulla and cortex of the distal tip. Phaeomelanin is restricted to the medulla in the distal quarter of the hair's length. To the eye, guard hairs have a black tip and pale yellow shaft, although occasionally the entire hair may appear black or the black tip may be lacking. There is virtually no difference between *sylvaticus* (B) and *krkensis* (C) in the overall structure of the guard hairs or the distribution of pigment, but once again the granules in *krkensis* are paler and fewer than in *sylvaticus*.

One noteable exception to this similarity in guard hairs involves the keratin secreted by the medullary cells. This proteinaceous support matrix forms a reticulated pattern within the medulla that is either of a pale bluish gray tint (hereafter referred to as "dark") or is colorless ("clear"). In *A. sylvaticus*, the dark reticulated pattern (indicated by cross-hatching in Fig. 4) predominates, whereas in *A. krkensis* it is considerably reduced. The upper right inset illustrates the sharp transition between the two types of keratin. The degree of dark as opposed to clear reticulation and its localization in the hair shaft is somewhat variable but the general relationship alluded to above holds. Although keratin does not affect the color per se, where the clear pattern occurs, light passes unimpeded through the hair, and the shaft reflects the color of the underlying underfur. For *A. krkensis* this means guard hairs, which have primarily clear reticulation, are essentially translucent, contribute little to total pelage coloration, and give the illusion of being gray when overlaying the gray hairs of the underfur. This is true even in the basal portion of the hair where pigment granules are concentrated most (see inset on lower right).

Discussion

Works on penial and bacular morphology (Williams et al. 1980), heterochromatic chromosomal C-banding patterns (Engel et al. 1973), and electrophoretic allozyme analyses (Engel et al. 1973; Darviche et al. 1979) have detected differences between *A. sylvaticus* and *A. flavicollis* that substantiate the findings of breeding studies, namely that the two taxa represent separate species. Zimmermann's (1957) classic observations on breeding behavior have indicated that pre-mating isolating mechanisms are strong between these two species and more important in preventing interspecific crosses than are post-mating mechanisms, although the latter do exist.

Despite detectable differences in the character states listed above, *A. sylvaticus* and *A.*

flavicollis are extremely similar and notoriously difficult to recognize when caught in the field. Soldatović et al. (1975) have shown that even standard karyotypes are identical with both species exhibiting a diploid and fundamental number of 48 (minor variation in diploid number was recorded by these authors for *A. flavicollis*). Accurate identification of these two taxa thus requires either using specialized techniques (electrophoresis, chromosome banding, etc.) or applying to morphological data sensitive statistical tests such as a multivariate analysis of variance. However, because it was impossible to differentiate a third nominal species, *A. krkensis*, from *A. sylvaticus* even by using Manova procedures, we conclude there are no observable differences in size or shape between *sylvaticus* and *krkensis*.

Mirić (1968), in his original description, compared *krkensis* only with *A. mystacinus*. He stated that *krkensis* resembled *mystacinus* by having a gray dorsal color and four lateral cusps on the first two upper molars. Regarding these similarities, the following points should be emphasized. Even though *krkensis* is gray in color it has a yellowish wash over the flanks that is lacking in *mystacinus*. Also, pelage texture is quite different – that of *krkensis* is short and coarse whereas in *mystacinus* it is long and silky. Furthermore, four lateral cusps are as well defined in young specimens of *A. sylvaticus* from the mainland and the islands of Krk and Rab as those depicted in Mirić's figure 7 (p. 374) for *A. krkensis*. Counting anteriorly to posteriorly, cusp 4 on M^1 and cusps 1 and 4 on M^2 become easily obscured by wear due to their small size, thus leading to the illusion of only three lateral cusps being present in older animals. It appears that lateral cusp number does not truly differ between purported specimens of *A. krkensis* and *A. sylvaticus*. Mirić also used the following traits to distinguish further *krkensis* from *mystacinus*: 1. masseteric plate perpendicular, not oblique; 2. parietal and frontal sutures forming an oblique angle, not a semicircle; 3. anterior orbital plate concave, not convex; 4. nasal bones concave, not straight or convex; 5. lateral process of palatine neither overlaying nor enclosing the palatine canal; 6. posterior protrusion of palatine lacking; 7. absence of a hamular process that extends posteriorly to the anterior border of the auditory bullae; 8. anterior border of the point of insertion for the masseter muscle reaching the mental foramen; 9. upper third molar bearing a lateral identation that is equal in depth to one-third of the tooth's breadth; 10. a gray rather than white venter.

The gray mice collected on the island of Krk for this study are considered here as topotypes of *A. krkensis* bescause they faithfully match the description of the pelage and exhibit every cranial and dental feature referred to above and ascribed by Mirić to the species *krkensis*. The fact that these topotypes share the same cranial and molar patterns with normally colored *sylvaticus* (that is, wood mice with a reddish dorsal pelage and grayish venter with an indistinct line delineating the two) examined from Labin, Lekenik, and Posedarje on the mainland and from the islands of Rab and Krk indicates to us that the characters assigned to *A. krkensis* by Mirić do not differentiate specimens of that nominal species from *A. sylvaticus*. A comparison of selected measurements for the holotype male, paratype female, and juvenile paratype male of *krkensis* with data for the topotypes caught during the course of this investigation are shown in Table 1. The reader can verify that there are no significant differences between these and the representative sample of *A. sylvaticus* included.

Although Mirić recognized *krkensis* as a distinct taxon, Niethammer (in Niethammer and Krapp 1978) reduced it to a subspecies of *mystacinus*. Our analysis shows that there are no particular size, shape, cranial, or dental differences between topotypes of *krkensis* and sympatric specimens of *A. sylvaticus*. Corbet (1978), after examining one of the topotypes, concluded that *krkensis* shared no particular affinity with *mystacinus* and in all likelihood was very closely related to *sylvaticus*.

While no demonstrable mensural differences can be seen between the gray and reddish field mice living on Krk, there definitely do exist two color phases. The variation in color,

as shown by Fig. 4, is primarily the result of a reduction in both the number of melanosomes and the amount of pigment contained therein in underfur hairs of the gray morph. Based on a review of aberrant pelage types for *A. sylvaticus* (Dolan and Carter, unpublished data) and an examination of the literature on specific genetic loci and their effect on pigment distribution and melanogenesis (Grüneberg 1952; Little 1958; Billingham and Silvers 1960; Foster 1965; Searle 1968), we propose a hypothesis for future testing: specifically, that the gray mice previously referred to as *krkensis* are merely pale color morphs of *A. sylvaticus* and that a mutation at the albino (= C) locus in the animal's genome to a "chinchilla"-like allele is responsible for the paling effect (see Grüneberg 1952: 28 for the action of this allele in *Mus musculus*). The validity of this proposal is open to confirmation or rejection by breeding studies.

The occurrence of pale colored wood mice at localities other than the island Krk further strengthens the argument advanced here that *krkensis* is conspecific with *sylvaticus*. Similarly gray mice were trapped in 1975 on the nearby island of Rab, and a single individual was taken the following year in the vincinity of the coastal town of Karlobag. We do not wish to imply that gray wood mice from Krk, Rab, and Karlobag share a similar coloration as a result of descendency from a common ancestral population. In fact, we are more inclined to view the appearance of these populations as examples of convergent events because there is some variation in the degree of paling among localities, which suggests different alleles at the C locus could be involved. The common denominator among these samples of mice seems to be the presence of highly reflective substrates. Without exception, gray mice were caught in habitats where vegetation was sparse but exposed limestone karst outcroppings were abundant. Correlations between pelage and soil type have been reported before by Howell (1920) for *Peromyscus polionotus* and Blair (1947) for *P. maniculatus*. Dice (1947) has shown that this matching of animal to substrate can be effective in reducing predation. It is quite possible that gray pelage confers a selective advantage to those wood mice inhabiting relatively barren areas and that this has led to its development and presistence along the northern Adriatic region of Yugoslavia.

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Zusammenfassung

Interspezifische Variation bei Apodemus von den nördlichen adriatischen Inseln Jugoslawiens

Mit Hilfe einer auf 14 Schädelmassen beruhenden, multivariaten Varianzanalyse konnten Wald- und Gelbhalsmäuse *(Apodemus sylvaticus* und *A. flavicollis)* aus Kroatien völlig getrennt werden. Hingegen fielen auf Grund ihrer grauen Färbung als *A. krkensis* identifizierte Mäuse von der Insel Krk ganz in den Wertebereich von *A. sylvaticus*.

Der unterschiedliche Farbeindruck bestätigte sich auch in einer spektrophotometrischen Analyse. Auch auf der Krk benachbarten Insel Rab wurden fast so helle Waldmäuse gefunden wie die als *A. krkensis* identifizierten. Der helleren Färbung entspricht eine verringerte Anzahl und Aufhellung der Melanosomen in den Wollhaaren von *A. krkensis*.

Nach diesen Befunden sind *A. sylvaticus* and *A. krkensis* wahrscheinlich konspezifisch.

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